Distribution and cycling of macronutrients in a *Pinus resinosa* plantation fertilized with nitrogen and potassium

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Fertilization with 100 kg K ha^{-1} as KCl and 100 kg N ha^{-1} as NH_4NO_3 resulted in an 11% increase in aboveground biomass and a 32% increase in aboveground production 4 years following fertilization of a 33-year-old red pine (*Pinus resinosa* Ait.) plantation in central Wisconsin. The greatest absolute increase in dry matter occurred in the foliage, followed by the sapwood and the live branches. Fertilization increased all macronutrients (N, P, K, Ca, Mg) in the aboveground tissues. The increase was greatest for N, followed by Ca, K, Mg, and P. The net gains in macronutrients in the live branches and the sapwood were due not only to increases in dry matter production but also to increases in nutrient concentrations. However, the increases in macronutrients in the foliage were related to an increase in foliage mass rather than to changes in foliar concentrations. Whereas 26 kg K ha^{-1} (26% of applied K) was recovered in the biomass and forest floor 4 years after fertilization, 107 kg N ha^{-1} (107% of applied N) was recovered in these pools. The greater recovery of N than the amount applied was attributed to additive errors associated with preparation of nutrient budgets. Fertilization increased leaching losses of all macronutrients, especially NO_3^- and Ca^{2+}, at the bottom of the rooting zone. However, leaching losses returned to levels measured in the control stand within 5 (K^+, NH_4^+) to 14 months (NO_3^-, Ca^{2+}) following fertilization.

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Une fertilisation avec 100 kg K ha^{-1} sous forme de KCl et 100 kg N ha^{-1} sous forme de NH_4NO_3 s'est traduite par une augmentation de 11% de la biomasse et une augmentation de 32% de la production épigée, 4 ans après traitment d'une plantation de pin rouge (*Pinus resinosa* Ait.) dans le centre du Wisconsin. La plus forte production de matière sèche était sous forme de feuillage, suivi par l'aubier et les branches vivantes. La fertilisation s'est traduite par une augmentation de tous les éléments majeurs (N, P, K, Ca, Mg) dans les tissus épigés. L'augmentation fut la plus forte pour N, suivi de Ca, K, Mg et P. Les gains nets d'éléments majeurs dans les branches vivantes et l'aubier ne sont pas dus uniquement à l'augmentation de matières sèches mais aussi à l'augmentation des concentrations en éléments. Cepedant, les augmentations en éléments majeurs du feuillage étaient reliées à l'augmentation de la masse du feuillage plutôt qu'aux changements des concentrations foliaires. Quatre ans après fertilisation, 26 kg Kha^{-1} (26% de K appliqué) furent recouvrés dans la biomasse et la couverture morte, comparativement à 107 kg N ha^{-1} (107% de N appliqué) pour l'azote. L'excès de récupération de N, par rapport à N appliqué, est attributé à des erreurs additives dans l'évaluation des budgets d'éléments. La fertilisation a augmenté les pertes par lessivage de tous les éléments majeurs au-delà de la zone d'enracinement, en particulier NO_3^- et Ca^{2+}. Cependant, le lessivage est revenu au niveau normal des témoins en dedans de 5 mois (K^+, NH_4^+) à 14 mois (NO_3^-, Ca^{2+}) suivant la fertilisation.

[Traduit par la revue]

Introduction

Macronutrients (N, P, and K) commonly are limiting in northern conifer stands (Armson *et al.* 1975). Although most of the fertilizer studies summarized by Armson *et al.* (1975) dealt with jack pine (*Pinus banksiana* Lamb), black spruce (*Picea mariana* (Mill.) B.S.P.), and balsam fir (*Abies balsamea* (L.) Mill.), several studies have been conducted on red pine (*Pinus resinosa* Ait.), an important timber species in the Great Lakes region. Leech (1967) reported a 64% increase in diameter growth of red pine in southern Ontario following fertilization with N in combination with P, K, and Ca. Application of P and lime increased volume growth of thinned and unthinned red pine in upper Michigan by 23 and 28%, respectively (Shetron and Botti 1984). Three years after fertilization with N + P + K, diameter increment of red pine in Minnesota increased up to 18% (Johnson *et al.* 1983). Dramatic and long-lived responses of red pine to K fertilization have been reported on sandy soils in New York (Heiberg *et al.* 1964; Leaf 1969; Leaf *et al.* 1975; Wittwer *et al.* 1975).

Most fertilization studies report the magnitude of fertilizer response in terms of diameter, basal area, or volume increment (Armson *et al.* 1975). Comerford *et al.* (1980) pointed out the limitations in using diameter and basal area increment from measurements at breast height (1.37 m) to estimate fertilizer response, showing that for red pine, the response may initially occur in the upper portion of the tree. Application of 448 kg K ha^{-1} increased aboveground biomass of red pine in New York 22% in 4 years (Wittwer *et al.* 1975). The greatest increase (70%) occurred in foliage, followed by live branches (20%), bole wood (15%), and bark (10%).

Few studies have estimated the recovery of applied fertilizers. Ballard (1979) summarized recovery of applied N, P, and K in *Pinus* ecosystems, reporting recovery values ranging from as low as 3% to as high as 102%. The variation in recovery values is dependent on (*i*) the degree to which the applied element was limiting, (*ii*) the method for estimating recovery, (*iii*) the length of the observation period (1–15 years), (*iv*) the rate and frequency of fertilizer application, and (*v*) the amount of fertilizer loss because of deep leaching and volatilization.

The objectives of the experiment were (*i*) to measure the response of red pine by tree tissue to application of N + K, (*ii*) to determine the efficiency of utilization of the applied N + K, and (*iii*) to estimate the effects of fertilization on nutrient cycling, including transfers as a result of litter fall, throughfall, stemflow, and forest floor leaching and leaching loss outputs.

Experimental area

The study area was described in a previous publication (Bockheim *et al.* 1983) and will only be highlighted here. The experimental area is an 8.4-ha mixed pine plantation in central Wisconsin (44°16′ N, 89°26′

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TABLE 1. Mean height (m) and total basal area ($m^2\ ha^{-1}$) for red pine on control and fertilized plots at the beginning and conclusion of the experiment

Treatment	1979		1983	
	Height	Basal area	Height	Basal area
Control	13.4	22.9	14.5	29.7
N+K	13.7	23.0	15.0	31.5

W). In 1980, prior to fertilization, the stand had a basal area of $22.9\ m^2\ ha^{-1}$: 86% was red pine, 11% was white pine (*Pinus strobus* L.), and 3% was jack pine. The stocking was 630 stems ha^{-1} and the site index of red pine was 19 m (base age, 50 years).

The stand is growing on a Plainfield loamy sand (mixed, mesic, Typic Udipsamment) derived from acid glacial outwash of late Wisconsin age (ca. 14 000 years before present (BP)). The climate is humid continental with warm, humid summers and cool, dry winters. The mean annual temperature is 7.1°C, with July and January means of 22 and −9.1°C, respectively. The mean annual precipitation is 740 mm.

Methods

Twenty-four 200-m^2 rectangular plots were established in the plantation prior to fertilization in the spring of 1980 before the 34th growing season. Each plot contained from 9 to 16 trees. Six fertilizer treatments, including N, K, N + K, K + Mg, N + K + Mg, and controls, were applied in a randomized block design. Each treatment was replicated four times. Nitrogen was applied at a rate of 100 kg ha^{-1} as NH_4NO_3, potassium at 100 kg ha^{-1} as KCl, and magnesium at 50 kg ha^{-1} as MgO–$MgSO_4$. The fertilizer was spread by hand in the late spring of 1980. Total height and diameter at breast height (dbh) were measured on each of 300 trees at the beginning of the experiment and four growing seasons following fertilization. At the end of 4 years, only the trees receiving N + K showed a significant response over the controls and, therefore, additional work was done only on red pine trees on these and the control plots. Mean height and basal area of N + K and control plots prior to and 4 years following fertilization are reported in Table 1.

Four growing seasons after fertilization (1983), aboveground biomass of control trees and fertilized trees was predicted for each tissue (current foliage, older foliage, current twigs, live branches, dead branches, bole bark, and bole wood) from separate sets of allometric equations relating mass of a given tissue to dbh and total height. Prior to fertilization, equations were developed for red pine trees on control plots and, following fertilization, equations were developed for fertilized trees. The sample trees, 10 on control plots and 9 on fertilized plots, represent the range of tree diameters on these plots. Details of the sampling procedure and calculations are given in Bockheim *et al.* (1983). The equations have the following form:

$$[1] \quad \log Y = a + b \log D + c \log H$$

where Y is the mass (kilograms per tree), D is the dbh (centimetres), H is the total height (metres), and a, b, and c are regression coefficients. The equations for control and fertilized (N + K) red pine are given in Table 2, along with the coefficients of determination (r^2) and standard errors of the estimate ($S_{y \cdot x}$). Although the equations were not corrected for bias due to logarithmic transformations, calculation of correction factors according to the method of Sprugel (1983) did not improve the estimates by more than 3% (Table 2).

The coarse + medium (>2 mm) root biomass (kilograms per hectare) for each treatment was estimated as the product of aboveground biomass (kilograms per hectare) and a ratio of root biomass (>2 mm) to aboveground biomass. The ratios were derived by excavating and weighing the root systems of one tree from each treatment for which aboveground biomass had been measured. For each treatment, biomass of fine roots (<2 mm) was estimated by wet sieving 48 cores measuring 6 cm in diameter and 30 cm in length. Total belowground biomass is the sum of coarse + medium and fine-root biomass.

Annual production of aboveground perennial tissues was estimated by subtracting biomass prior to the 1980 growing season from that in 1983 and dividing by 4 years. Production of fine roots was estimated as 80% of fine-root biomass (McClaugherty *et al.* 1982). Production of roots >2 mm was estimated using the following assumed relationship (Whittaker and Marks 1975):

$$[2] \quad \frac{\text{annual root production (>2 mm)}}{\text{root biomass (>2 mm)}} = \frac{\text{aboveground production}}{\text{aboveground biomass}}$$

Tissue samples were collected from each of the 19 red pine trees sampled for biomass. Tissues were dried at 65°C and ground in a laboratory mill. The ground tissues were combusted in a muffle furnace at 500°C for 16 h and a subsample was dissolved in concentrated HNO_3 and $HClO_4$. The solutions were analyzed for P, K, Ca, and Mg by the Wisconsin Soil and Plant Analysis Laboratory on an inductively coupled plasma emission spectrometer (Genson *et al.* 1976). Total N was determined on a ground subsample using a semimicro-Kjeldahl apparatus.

Nutrient content of red pine trees was determined by summing the products of dry matter content, nutrient concentrations, and a stocking factor for each tissue and treatment.

Twenty-four forest floor samples measuring 0.25 m^2 were collected in a systematic grid from control and N + K plots in the fall of 1983 and analyzed as tissue samples. Composite (four) bulk soil samples were collected from horizons of four profiles on control and four on N + K plots in the fall of 1983. Volumetric samples were taken from horizons of two profiles for bulk density determinations. The following chemical analyses were made on bulk soil samples: easily oxidizable organic carbon by the Walkley–Black procedure; total N by semimicro-Kjeldahl; exchangeable Ca, Mg, and K following extraction with 1 N ammonium acetate (pH 7.0); and P following extraction with 0.002 N sulfuric acid (Wilde *et al.* 1979).

Two of each of the following collectors were placed on three plots per treatment: throughfall, stemflow, litter fall, forest floor leachate (7.5 cm), and deep soil leachate (55 cm). In addition, three precipitation collectors were placed in open areas adjacent to the stand. Design of the throughfall and precipitation collectors is described by Hart and Parent (1974). Stemflow and litter fall collectors were similar to those used by Foster (1974). Soil leachates were collected using porous ceramic cups manufactured by Soil Moisture Equipment Corporation. Solutions and litter fall samples were collected for the first 2 years following fertilization (June 1980 to May 1982) at approximately 2-week intervals during the period from April 15 to November 15. When permanent snow cover was present, monthly snowfall samples were collected in the open. Solutions were analyzed for NH_4^+ and NO_3^- on a Technicon autoanalyzer, K^+ on a flame photometer, and Ca^{2+} and Mg^{2+} on an atomic absorption spectrophotometer. Calcium and magnesium values may be somewhat low because no interference suppressant was added to solution samples. Procedures followed for water analysis are given in Anonymous (1975). Organic N was estimated on solution samples by subtracting NH_4 N from measurements of total Kjeldahl N. Annual fluxes of each component were computed by taking the product of volume and concentration of the solutions and adding the values for a given budget year. Volume of the forest floor leachate was assumed to be 98% of the net precipitation (throughfall + stemflow). Volume of the deep soil leachate for each sampling period was estimated by the method of Thornthwaite and Mather (1957).

Fertilizer recovery was estimated by the accounting method of Miller *et al.* (1976):

$$[3] \quad R = 100 \times ((B_{N+K} - B_{CO}) + (F_{N+K} - F_{CO}))/\text{amount of fertilizer applied}$$

where R is the accounting estimate of percent recovery, B_{N+K} and B_{CO} are the nutrient contents (kilograms per hectare) of above- and below-ground biomass of the fertilized and control plots, respectively,

TABLE 2. Biomass equations* for control (CO) and fertilized (N+K) red pine in central Wisconsin

Component	Treatment	a	b	c	CF	r^2	$S_{y \cdot x}$
Foliage	CO	−0.958	2.29	−0.894	1.01	0.935	0.0712
	N+K	0.601	2.23	−1.97	1.02	0.343	0.0979
Live branches	CO	−2.22	3.21	−0.647	1.02	0.951	0.0870
	N+K	0.889	2.60	−2.57	1.03	0.325	0.113
Dead branches	CO	8.24	6.34	−14.20	1.10	0.844	0.185
	N+K	−20.60	2.53	14.90	1.50	0.465	0.391
Bole bark	CO	−2.42	1.63	1.05	1.00	0.975	0.0346
	N+K	−2.67	1.66	1.24	1.00	0.954	0.0232
Bole wood	CO	−2.18	1.70	1.67	1.00	0.999	0.0074
	N+K	−2.01	1.88	1.32	1.00	0.977	0.0181
Aboveground total	CO	−1.56	2.00	0.918	1.00	0.995	0.0189
	N+K	−0.957	2.05	0.377	1.00	0.939	0.0282

*Equation form: $\log Y = a + b \log D + c \log H$, where Y is mass (kilograms per tree), D is diameter at breast height (centimetres), H is total height (metres), a, b, and c are regression coefficients, CF is the correction for bias in regression estimates due to logarithmic transformation (Sprugel 1983), r^2 is the coefficient of determination, and $S_{y \cdot x}$ is the standard error of the estimate $\log_{10}$ (n = 10 for CO, n = 9 for N + K).

TABLE 3. Dry matter and nutrient contents (kg ha^{-1}) of a 37-year-old red pine plantation not receiving a fertilizer application

Component	Organic matter	N	P	K	Ca	Mg
Vegetation						
Bole wood	80 700	75	9.4	27	72	17
Bole bark	7 070	26	3.8	7.4	46	4.7
Live branches	18 600	58	9.0	24	93	12
Dead branches	2 880	6.0	0.5	0.6	11	1.2
Foliage	9 690	110	14	47	37	12
Aboveground total	119 000	275	37	106	259	47
Roots	40 400	106	20	57	59	22
Total	159 000	381	57	163	318	69
Forest floor	20 670	223	17	17	160	14
Soil*						
Ap, 0–18 cm	25 900	1332	10	23	365	48
Bw-1, 18–36 cm	15 700	1385	7.6	20	408	50
Bw-2, 36–60 cm	11 300	1076	15	28	481	39
Total	52 900	3800	33	71	1250	137
Ecosystem total	233 000	4400	107	251	1700	220

*Parameters measured in the soil are total N, extractable P, and exchangeable K, Ca, and Mg.

4 years after fertilization, and F_{N+K} and F_{CO} are the nutrient contents (kilograms per hectare) of the forest floor in the fertilized and control plots, respectively.

Results and discussion

Biomass and net primary production

Allometric equations for predicting biomass for each tree component in control and fertilized stands are given in Table 2. Preliminary analysis showed that inclusion of height in the equations improved the coefficients of determination and standard errors of the estimate for predicting the biomass of the bole bark, the bole wood, and the total aboveground portion of the tree, but did not improve the equations for predicting the biomass of foliage and live branches. The r^2 values were lower and the standard errors of the estimate ($S_{y \cdot x}$) were greater for components of the fertilized trees relative to those for the control trees. The equations for predicting biomass of foliage and live branches of fertilized trees were weaker than those for control trees.

Dry matter distribution for red pine on the control and fertilized plots at age 37 years (4 years after fertilization) are shown in Tables 3 and 4, respectively. Whereas dry matter was 159 Mg ha^{-1} in the control plots, total dry matter in the plots fertilized with N + K was 175 Mg ha^{-1}, or 10% greater. Fertilization slightly increased the dry matter content of aboveground tissues, particularly the foliage. Dry matter distribution in the control and fertilized stands was as follows: bole wood > roots > live branches > foliage > bole bark > dead branches.

Annual aboveground production for the control and fertilized plots averaged over 4 years was 11.8 and 15.6 Mg ha^{-1} year^{-1}, respectively (Table 5). Production in the fertilized plots was 32% greater than in the controls. More than half of the aboveground production was in sapwood, followed by current

TABLE 4. Dry matter and nutrient contents (kg ha^{-1}) of a 37-year-old red pine plantation 4 years after fertilization with 100 kg N ha^{-1} and 100 kg K ha^{-1}

Component	Organic matter	N	P	K	Ca	Mg
Vegetation						
Bole wood	84 360	81	10	30	74	18
Bole bark	7 340	23	3.2	8.2	46	4.9
Live branches	21 220	102	15	45	159	18
Dead branches	2 100	6.9	0.5	0.5	12	0.8
Foliage	16 510	182	21	67	81	20
Aboveground total	132 000	395	50	151	372	62
Roots	43 400	111	15	41	51	20
Total	175 000	506	65	192	423	82
Forest floor	18 300	205	14	14	116	12
Soil*						
Ap, 0–22 cm	37 500	1706	11	30	233	25
Bw-1, 22–37 cm	12 600	972	5.4	18	151	18
Bw-2, 37–60 cm	6 000	750	10	39	352	51
Total	56 100	3400	26	87	740	94
Ecosystem total	249 000	4100	105	293	1280	188

*Parameters measured in the soil are total N, extractable P, and exchangeable K, Ca, and Mg.

foliage or live branches, and bole bark. Over 4 years, the percent increase in live branch production was greater than that of foliar production.

Belowground production in both the control and fertilized plots was 11 Mg ha^{-1} year^{-1} (Table 5). Fine-root production (<2 mm) for both treatments was 7.5 Mg ha^{-1} year^{-1}. Total production in the control and fertilized plots was 22.4 and 27.1 Mg ha^{-1} year^{-1}, respectively (Table 5). Fine-root production contributed 33% of the total production in control plots and 27% in the fertilized plots. These values are similar to those reported by Keyes and Grier (1981) for *Pseudotsuga menziesii* (Mirb.) Franco and Grier *et al.* (1981) for *Abies amabilis* (Dougl.) Forbes in western Washington.

Nutrient distribution

Fertilization increased the contents of macronutrients (N, P, K, Ca, and Mg) in the total aboveground biomass (cf. Tables 3 and 4). The increase over control was greatest for N and Ca (44%), followed by K (42%), P (35%), and Mg (32%). The greatest increases in macronutrients of fertilized trees over controls occurred in the live branches and foliage. Whereas the increases in macronutrients in the live branches were due primarily to greater concentrations of macronutrients in the live branches of fertilized trees (Table 6), the increases in macronutrients in the foliage were due primarily to an increase in dry matter. Based on a simple *t*-test, concentrations of all macronutrients were significantly greater in the live branches of trees fertilized with N + K than in control trees. In addition, concentrations of N, P, K, and Mg were significantly greater in sapwood production (1979–1983) of fertilized trees relative to the controls.

These same trends are apparent in net primary production (NPP) (Table 5). Whereas aboveground NPP was 32% greater in the fertilized stand than in the control stand, nutrient content of aboveground NPP in the fertilized plots was 40 to 82% greater than in the control plots.

Because the roots of only one control tree and one tree fertilized with N + K were sampled, no statistical comparisons of the treatments could be made. In general, concentrations of macronutrients decreased with an increase in root diameter (Table 6). In addition, the concentrations of N in roots less than 30 mm in diameter, particularly in fine roots (<2 mm), were greater for the fertilized tree than for the control tree.

There were no significant differences in dry matter content and macronutrient concentrations of the forest floor between control and fertilized plots, except for a greater concentration of Ca in the forest floor of the control plots. The total quantities of macronutrients in the forest floors of the fertilized plots were less (significantly less only for Ca) than in the control plots (Tables 3 and 4).

Amounts of macronutrients in the soils of the control and fertilized plots are reported in Tables 3 and 4, respectively. For both the control and fertilized plots, the greatest proportions of the total N and available Ca and Mg were in the mineral soil. In contrast, the greatest proportions of available P and K were in the vegetation.

Nutrient transfers

Precipitation supplies 11.6 and 4.3 kg ha^{-1} year^{-1} of N and K, respectively (Table 7). Fertilization increased leaching losses of all macronutrients measured the first 2 years following fertilization. The losses were greatest for N (especially NO_3^-) and Ca^{2+}. Concentrations of NH_4^+ and K^+ in deep soil leachates returned to levels measured in the control plots 5 months after application (Figs. 1 and 2). In contrast, NO_3^- and Ca^{2+} required 14 months to return to control levels. Whereas net inputs of N, K, and Ca in bulk precipitation exceeded leaching loss outputs in the control plots, the reverse was true for N and Ca in the plots fertilized with N + K (Table 7). Otchere-Boateng and Ballard (1978) reported an increase in concentrations of cations, particularly Ca^{2+} and Mg^{2+} in deep soil leachate, following application of 448 kg N ha^{-1} as urea, and attributed these losses to a decline in solution pH accompanying nitrification in fertilized plots. We report a similar decline in pH following fertilization (Fig. 3).

Fertilization slightly increased the N and K contents of aboveground litter fall and throughfall (Table 7). Mahendrappa and Ogden (1973) likewise reported small increases in the N content of litter fall (2.2 kg ha^{-1} year^{-1}) and throughfall (0.6 kg ha^{-1} year^{-1}) beyond values in control stands 1 year after

TABLE 5. Dry matter and nutrient (kg ha^{-1} $year^{-1}$)* contents of net primary

Tissue	Dry matter			N			P		
	CO	N + K	Difference	CO	N + K	Difference	CO	N + K	Difference
Sapwood	6 400	8 230	1830(29)†	8.3	13	4.7(57)	1.1	1.7	0.6(55)
Bole bark	485	620	135(28)	1.8	1.9	0.1(6)	0.3	0.3	0(0)
Live branches	2 070	3 380	1310(63)	6.6	16	9.4(142)	1.0	2.4	1.4(40)
Current foliage	2 900	3 410	510(18)	32	38	6.0(19)	4.4	5.1	0.7(16)
Total	11 800	15 600	3780(32)	49	69	20(41)	6.8	9.5	2.7(40)
Roots	10 600	11 400	845(8)	43	55	12(28)	9.8	7.2	−2.6(26)
Total	22 400	27 100	4630(21)	92	124	32(35)	17	17	0(0)

*Average of first 4 years after fertilization, i.e., 1979–1983.
†Percent differences are shown in parentheses.

TABLE 6. Concentrations (%) of macronutrients in tissues of control

Component	N		P	
	CO	N + K	CO	N + K
Current foliage	1.12(0.023)*	1.12(0.014)	0.154(0.0029)	0.153(0.0024)
Older foliage	1.16(0.026)†	1.09(0.014)	0.133(0.0013)†	0.111(0.0014)
Current twigs	0.82(0.054)	0.82(0.045)	0.138(0.0093)	0.148(0.0076)
Live branches	0.32(0.021)	0.48(0.014)†	0.048(0.0022)	0.070(0.0024)†
Dead branches	0.21(0.020)	0.33(0.028)†	0.017(0.0029)	0.022(0.0020)
Bole bark	0.36(0.021)	0.31(0.017)	0.053(0.0036)	0.044(0.0032)
Sapwood production	0.13(0.0078)	0.16(0.0040)†	0.018(0.0006)	0.021(0.0008)†
Bole wood	0.074(0.0080)	—	0.012(0.0019)	—
Roots				
<2 mm	0.49	0.67	0.12	0.088
2–5 mm	0.40	0.54	0.074	0.076
5–10 mm	0.32	0.47	0.057	0.063
10–30 mm	0.22	0.33	0.035	0.034
>30 mm	0.15	0.16	0.028	0.020
Stump	0.19	0.090	0.024	0.010

*Standard errors are shown in parentheses.
†Statistically greater at $P < 0.05$ based on simple t-test; all others are not statistically different (except roots, where there was insufficient

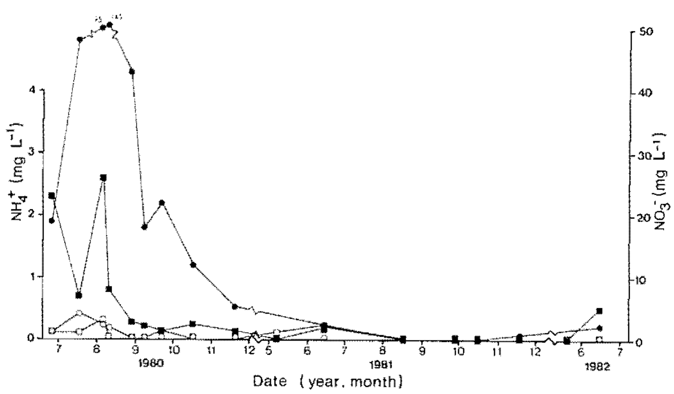

FIG. 1. Seasonal changes in the concentrations of NO_3^- (●, ○) and NH_4^+ (■, □) in the deep soil leachates in control (○, □) and fertilized (●, ■) red pine in central Wisconsin.

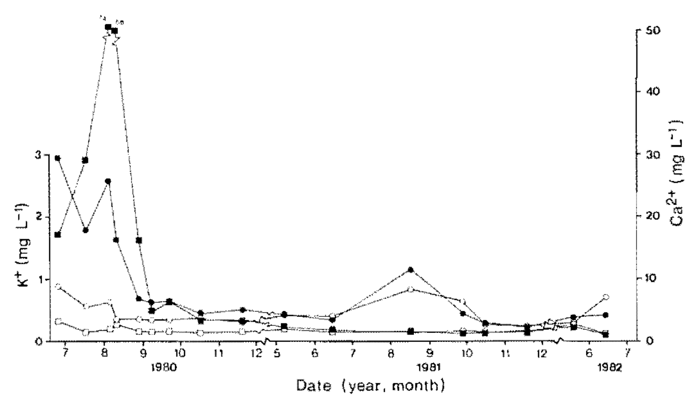

FIG. 2. Seasonal changes in the concentrations of K^+ (●, ○) and Ca^{2+} (■, □) in the deep soil leachates of control (○, □) and fertilized (●, ■) red pine in central Wisconsin.

application of 168 kg N ha^{-1} to a 60-year-old black spruce stand in New Brunswick. Yawney *et al.* (1978) reported slight (0.06–0.21 kg ha^{-1}) increases in the K content of throughfall + stemflow in a 39-year-old red pine plantation 2 years after fertilization with 448 kg K ha^{+} as KCl.

Recovery of applied N and K

Although the final disposition of the applied fertilizer elements in this study was not tracked using radioactive tracers, we estimated nutrient recovery by subtracting the total amounts of N and K in the biomass and forest floor of the control plots from that in the fertilized plots 4 years after fertilization (Eq. 3); 26% of the K and 107% of the applied N were accounted for 4 years after fertilization (Table 8). Adding the differences in leaching losses of N and K between the fertilized and control plots increases these estimates to 28 and 129% of the applied K and N, respectively. The soil on the fertilized plots contained

production for control (CO) and fertilized (N + K) red pine in central Wisconsin

K			Ca			Mg		
CO	N + K	Difference	CO	N + K	Difference	CO	N + K	Difference
3.1	6.2	3.1(100)	4.2	5.5	1.3(31)	1.1	1.7	0.6(55)
0.5	0.7	0.2(40)	3.1	3.9	0.8(26)	0.3	0.4	0.1(33)
2.7	7.1	4.4(163)	10	25	15(150)	1.3	2.8	1.5(115)
16	18	2.0(12)	6.7	9.2	2.5(37)	3.5	4.1	0.6(17)
22	32	10(45)	24	44	20(82)	6.2	9.0	2.8(45)
26	18	−8(31)	21	21	0(0)	11	9.3	1.7(15)
48	50	2(4)	45	65	20(4)	17	18	1.1(6)

(CO) and fertilized (N+K) red pine 4 years after fertilization

K		Ca		Mg	
CO	N + K	CO	N + K	CO	N + K
0.561(0.024)	0.543(0.016)	0.23(0.0078)	0.27(0.0072)†	0.115(0.0018)	0.117(0.0019)
0.415(0.0078)	0.393(0.0075)	0.53(0.020)	0.62(0.024)†	0.139(0.0034)†	0.128(0.0034)
0.34(0.022)	0.41(0.018)†	0.35(0.023)	0.36(0.0081)	0.107(0.0044)	0.115(0.0046)
0.128(0.0039)	0.211(0.0098)†	0.50(0.018)	0.75(0.020)†	0.065(0.0016)	0.084(0.0022)†
0.021(0.0026)	0.024(0.0028)	0.37(0.058)	0.57(0.066)	0.037(0.0059)	0.037(0.0056)
0.105(0.0099)	0.107(0.0060)	0.64(0.047)	0.59(0.026)	0.067(0.0047)	0.067(0.0035)
0.048(0.0026)	0.073(0.0026)†	0.066(0.0028)	0.067(0.0025)	0.017(0.0007)	0.020(0.0008)†
0.027(0.0022)	—	0.089(0.0020)	—	0.021(0.0012)	—
0.31	0.20	0.23	0.24	0.13	0.11
0.20	0.25	0.18	0.18	0.090	0.093
0.17	0.19	0.16	0.19	0.073	0.078
0.12	0.11	0.11	0.14	0.048	0.052
0.091	0.078	0.087	0.090	0.029	0.027
0.076	0.044	0.13	0.070	0.030	0.022

sampling).

TABLE 7. Nutrient fluxes (kg ha^{-1} $year^{-1}$) in control (CO) and fertilized (N + K) red pine in central Wisconsin (June 1980 to May 1982)

	N		K		Ca		Mg	
Component	CO	N + K	CO	N + K	CO	N + K	CO	N + K
Input								
Precipitation	11.6		4.3		9.1		1.1	
Output								
Leaching loss (55 cm)	1.8	15	1.3	1.8	7.0	28	1.9	6.2
Transfers								
Litter fall	21	23	4.9	5.6	29	29	4.7	4.6
Throughfall	15	15	5.6	6.3	9.9	11	1.7	1.9
Stemflow	0.1		0.08		0.1		0.02	
Forest floor leachate (7.5 cm)	5.1	121	7.3	120	15	32	7.6	11

16 kg ha^{-1} greater exchangeable K than the soil on the control plots. The failure to account for the remaining 56% of the applied K may be attributed to K fixation and errors in the budgeting procedure. Heiberg *et al.* (1959) recovered 34% of the applied K (112 kg ha^{-1}) in the tree biomass 9 years after fertilization in a 27-year-old red pine plantation in New York. Leaf and Berglund (1969) recovered 19% of the applied K (448 kg ha^{-1}) in the aboveground biomass 3 years after fertilization in a 40-year-old red pine stand in New York. Stone and Kszystyniak (1977) estimated 45–50 kg of the K applied (112 kg ha^{-1}) to be present in the mineral soil of a 41-year-old red pine plantation in New York.

TABLE 8. Accounting estimate of recovery (kg ha^{-1}) of applied fertilizer in a 37-year-old red pine plantation in central Wisconsin

	N				K			
Parameter	N + K	CO	Difference	% of applied	N + K	CO	Difference	% of applied
Biomass	506	381	125	125	192	163	29	29
Forest floor	205	223	−18	−18	14	17	−3	−3
Accounting recovery*	711	604	107	107	206	180	26	26
Leaching loss	26	3.6	22	22	3.7	1.6	2.1	2.1
Accounting recovery + leaching loss	737	608	129	129	210	182	28	28

*From Eq. 3 (Miller *et al.* 1976).

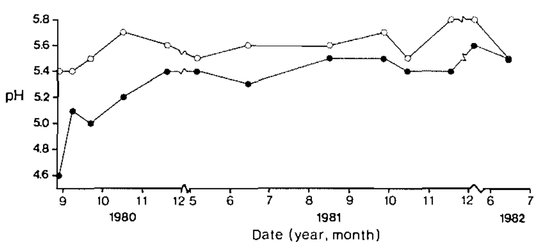

FIG. 3. Seasonal changes in pH of the deep soil leachates in control (○) and fertilized (●) red pine in central Wisconsin.

TABLE 9. Mean and approximate minimum standard deviations for N content (kg ha^{-1}) of tree tissues and the forest floor of fertilized (N + K) 37-year-old red pine plots in central Wisconsin

Component	N content
Vegetation	
Bole wood	81±31
Bole bark	23±3.7
Live branches	102±14
Dead branches	6.9±2.6
Foliage	182±11
Aboveground total	395±36
Roots	111±11
Total	506±38
Forest floor	205±66
Ecosystem total	711±76

The greater recovery of N than what was applied is difficult to explain. Miller *et al.* (1976) recovered 102% of the applied N (84 kg ha^{-1} year^{-1}) in the vegetation and the forest floor 3 years after fertilization of a pole-sized Corsican pine (*Pinus nigra* var. *maritima* (Ait.) Melv.) stand in Scotland. However, substantially lower recoveries of applied N generally are reported in the literature (Ballard 1979; Keeney 1980). The increased amount of N recovered over that applied may be due to (*i*) additive errors related to determination of the N contents of the various tree tissues and forest floor and (or) (*ii*) increased N mineralization in the upper part of the mineral soil as a result of fertilization. To test the first hypothesis, a conservative estimate of the error in the N content of the vegetation and forest floor pools of the fertilized plots was made. Standard deviations for the N content of the forest floor and of individual tree tissues and for the sums of those N contents were calculated assuming independence among all parameters. Because there is most certainly some correlation among these parameters, the error estimate is simply an indicator of the minimum error of the N recovery accounting. For the fertilized plot, this minimum estimate of the relative error of the calculated N content of tree tissues and the forest floor was 11%, i.e., 711 ± 76 kg N ha^{-1} (Table 9). Miller *et al.* (1976) reported an error of 12%. Therefore, the error associated with the nutrient budgeting approach is likely sufficient to result in recovery estimates in excess of 100% of the applied N.

There is some evidence in the literature to support the hypothesis that application of N fertilizer may stimulate N mineralization, which has been termed the "priming effect." Addition of $^{15}NH_4^+$ and $^{15}NO_3^-$ resulted in increased mineralization of organic N bound in the humus of a Norway spruce (*Picea abies* L.) stand (Overrein 1967). Similarly, Williams (1972) observed a twofold increase in net N mineralization from plots treated with urea or ammonium salts (250 kg N ha^{-1}) over controls in a Scots pine (*Pinus sylvestris* L.) stand in Scotland. However, Knowles (1975) cited numerous studies involving ^{15}N in which the release of humus N as extractable NH_4^+ was roughly equal to the $^{15}NH_4^+$ converted to nonextractable organic N.

In view of the uncertainty in the literature regarding effects of N fertilization on N mineralization, we favor the first hypothesis, i.e., additive errors in the nutrient budgets, as an explanation of the greater accounting estimate of recovery of N than that applied to the fertilized stand.

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